

DICKINSONIA: POLYCHAETE WORMS FROM THE LATE PRECAMBRIAN
EDIACARA FAUNA, SOUTH AUSTRALIA

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ABSTRACT

Dickinsonia is an extinct genus of errant polychaetes which dominated the South Australian late Precambrian Ediacara fauna. Like Recent *Spinther* they were characterized by the anterior body segment being fused around and in front of the prostomium. Neuropodia were reduced and phylogenetically lost in *Dickinsonia*, probably as the worms outgrew the range of width at which these appendages could function efficiently for locomotion. Freed from reliance on neuropodia, the widest worms ever known were produced, and segment length shortened. New material allows the removal of some of the specimens initially assigned to *D. tenuis* Glaessner and Wade to the new species *D. lissa* and *D. brachina*.

The genus *Dickinsonia* is the most common taxon in the Ediacara fauna in the Adelaide Geosyncline (Glaessner, 1961; Wade, 1968, table 1). The fauna occurs in a short stratigraphic interval not far above the base of the upper member of the Pound Quartzite (Wade, 1970) which Forbes (1971) has named the Rawnsley Sandstone Member. The areas where *Dickinsonia* has been collected are marked 1–7 on Fig. 1, which shows the distribution of the Pound Quartzite in the central Flinders Ranges where it occurs widely beneath a major unconformity capped by basal Lower Cambrian rocks of the Parachilna Formation (Dalgarno, 1964; Wade, 1970). Mr J. C. Gehling (pers. com.) has since found the fauna to the east of the area studied by Wade, at Reaphook Hill (7), and Dr B. Daily has traced it further to the east in the Mt Scott Range syncline (3).

In all, about 400 specimens of *Dickinsonia* have been collected; the vast majority of them are *D. costata* Sprigg. This is now known in growth stages from 7 to over 112 (approximately 120) segments; it is the only form in which some of the internal structures can be demonstrated. Comparison with *Spinther*, the only similar modern worm, shows that *D. costata* is the most generalized of the known Dickinsoniid worms; all other species show, in various more exaggerated forms, a trend to increasing numbers of short segments.

The short-segmented forms initially grouped as *D. tenuis* Glaessner and Wade are considered as three species now that better-preserved material of the narrower forms is available. *D. tenuis sensu stricto* is the broadest. The segments of *D. lissa* sp. nov. are sometimes a little longer (segment length is measured parallel to the axis of the worm), much narrower, and taper less toward their centres than in *D. tenuis*, and more are

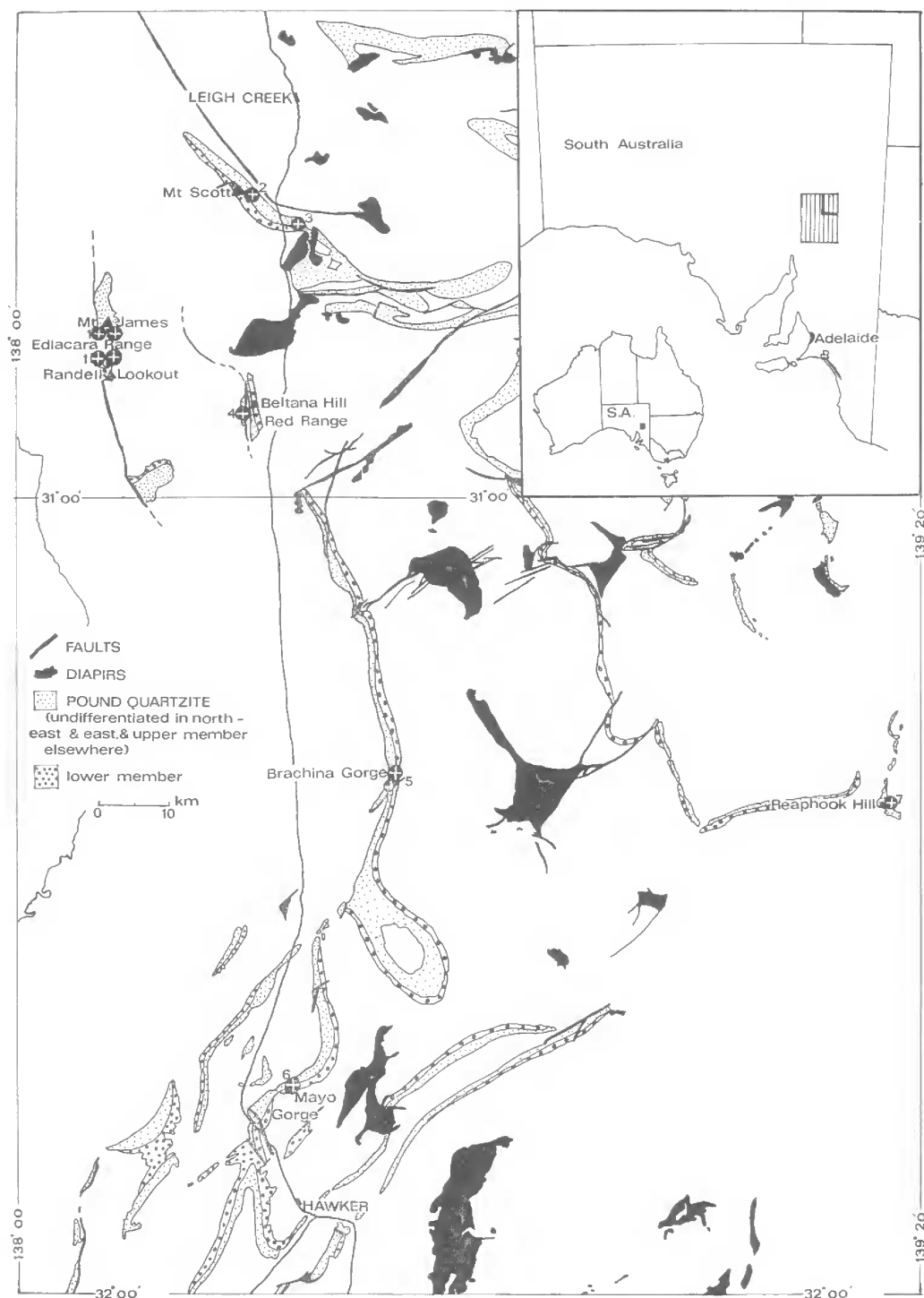


FIG. 1: Locality plan of the Flinders Ranges and adjacent areas showing the presently known distribution of *Dickinsonia*. All known occurrences are low in the upper member of the Pound Quartzite, the Rawnsley Sandstone Member.

transversely placed. *D. brachina* is very rare. It resembles *D. elongata* in all characters except segment length, which is as short as in large *D. lissa*, and its smaller overall size. All but one specimen of the new species (a positive composite mould of *D. lissa*) are at least partly impressions on the depositional bases of rock slabs, as are all *D. elongata* and *D. costata* (except for natural counterpart casts from accompanying impressions). *D. tenuis* and *D. lissa* are the only forms soft-bodied enough to occasionally form casts or positive composite moulds (Wade, 1968, table 1—*D. lissa* is the form referred to as 'unnamed dickinsoniid worm').

Evidence of the worms having been alive where deposited is of two main kinds, (1) worms which have been buried in a state of extreme contraction which is shown by a standard pattern of surface wrinkles produced on the fossils (Plate 5, figs. 3, 4), and (2) worms surrounded by areas from which they have contracted before burial (Wade, 1968, fig. 27; herein, Plate 5, fig. 1). No markings attributable to locomotion are known. The assemblage of five species of these worms is a thanatocoenosis (Wade, 1968, p. 266) and so does not imply that they competed for the same ecological niche.

The worms are here described as seen in latex casts (or in natural positive relief).

DEPOSITORIES. Original material is deposited in the collections of the Geology Dept., University of Adelaide, and the South Australian Museum, save for one each in the collections of R. J. F. Jenkins and a schoolboy collector. Registration numbers commencing T or F refer to the collections of the Geology Department, University of Adelaide, those commencing P refer to collections of the South Australian Museum.

THE SPECIES OF *DICKINSONIA*

I. *DICKINSONIA* WITH RELATIVELY LONG SEGMENTS

***Dickinsonia costata* Sprigg, 1947**

(Fig. 3; Plate 5, figs. 1–8; Plate 6, figs. 1–4)

A complete synonymy of the species was given by Glaessner and Wade (1966). Latex casts of about 100 of the better preserved specimens have been used in this study but practically all of the 350 or more collected have been examined. They come from localities 1–7 on Fig. 1, and the majority remain at The University of Adelaide and the South Australian Museum.

MORPHOLOGY

These worms are flat and elongate-ovate to wider than long. The posterior end is almost always notched at the axis and the anterior end is usually convex but rarely indented. The segmentation is clearly marked on both dorsal and ventral surfaces and the margin is incised between the segments. Segment size diminishes to the posterior, frequently to several times smaller than the more anterior segments. Throughout, the segments are individually longest at their free edges (tips) and shortest at their centres. The most anterior body segment is fused around and in front of the prostomium, and other anterior segments curve forward progressively less (as follows from the centrally-tapering segment shape),

making a series of widening, U-shaped ridges and depressions across the bodies. A variable but not large number of segments are nearly transverse about mid-length of the body, and the posterior segments slope progressively more sharply backward in a series of V-shaped ridges and depressions.

If the area around the posterior notch is well spread out, the most posterior pair of structures are seen to be shorter and broader than the adjacent half-segments, and biconvex (Plate 6, fig. 3, a). As they are always small, nearly flat, and rather obscure it is not possible to be conclusive about the original structure but the shape seen could be produced by flattening a pair of inflated anal lobes similar to those of *Spinther arcticus* Sars (Graff, 1888, as *S. 'miniaceus'* vide Hartman, 1948; Manton, 1967).

Segment surfaces present two main appearances: either they are delimited by furrows continuous from one side of the body to the other (in small specimens these may be indistinct near the centre), or they are clearly interrupted (even in small specimens) by an axial structure of variable width which is broader in more expanded specimens. Expansion is discussed on pp. 176–7. The sides with axially interrupted segments were considered dorsal (Wade, 1968, pp. 262–3), and new material of excellent preservation from Brachina Gorge in the main Flinders Ranges has enabled their notopodial-elytral ridges to be observed more clearly than previously (Plate 5, fig. 2; Plate 6, fig. 3).

Plate 5, fig. 1 shows two fairly large specimens on one slab, both are seen from the dorsal side and they have almost the same number of segments. Both have contracted from their maximum expansion in the place where they were deposited. The larger still appears quite well expanded, its profile is very flat, its septal sutures are not convincingly demonstrable, though their position can be inferred from the incised margins (Plate 5, fig. 2.), and its notopodial-elytral ridges are very sharply defined and end to either side of an axial ridge. This ridge dies out toward the anterior. The notopodial-elytral ridges are mostly folded backward but some are partly bent forward. They broaden rapidly toward their outer ends (notopodial portion) and form a fanshaped tip to each segment. In places these fanshaped tips overlie each other with the more anterior fans above the more posterior. The notopodial-elytral ridges of the first segment are quite widely separated at their inner ends, so that they cannot have reached to the apex of the segment. The ridges of the second segment extend further back but are similarly widely separated at their inner ends, and the following 3 segments also make a group whose ridges do not reach as near to the axial region as the remaining 56 segments. Plate 5, fig. 1 shows on specimen b a small, circular spot that occupies an axial position about the apex of the first segment (at arrow). On the original of fig. 1, a, and fig. 2, a similar spot overlaps a chance lump on the body. It is tempting to regard these circular spots as prostomia or prostomial tentacles like the short, thick 'tentacle' that covers the prostomium itself in *Spinther* but in no specimen is it clearly preserved, and outward expression of the prostomium remains a probability which is very difficult to quantify. It is possible that any kind of lump on or in the body gives rise to a circular 'pressure spot' so that structures in the position of the probable prostomium and/or mouth and pharynx are common in well-preserved specimens, but are often accompanied by similar spots that are haphazardly distributed.

The clearest of the structures possibly representing the mouth (or a wrinkle of extruded pharynx) is shown by the ventral side T50; 2001 (Plate 5, fig. 5; Sprigg, 1949, pl. 2, fig. 4;

refigured Harrington and Moore, 1956, fig. 15, 1b). In this and other specimens the presumed peristome is a short distance anterior to the U-shaped closure of the anterior body segment, i.e. a little anterior to the position of the probable prostomial tentacle seen in dorsal view.

Several ventral sides are of exceptionally good preservation though relatively small, and there are well-preserved portions of the margins of larger ventral-side specimens. Although all have been examined for any evidence of neuropodia it remains inconclusive. Certainly there are no large structures in this region. Some small lumps or flat, round spots near the segments tips could represent neuropodia but they are not constantly present. The two most distinctive examples are Plate 5, fig. 6 and Plate 6, figs. 1, 2. The original of Plate 5, figs. 3, 4 does not show a row of neuropodial bosses at the anterior left, as was initially thought possible, for the similar structures at anterior right occur in 2–3 rows; the zig-zag median furrow on its axial ridge indicates that it is a dorsal side. Some specimens have exceptionally long segments which are therefore large at the tips but these lack evidence of neuropodia. If present, neuropodia must have been small, and not closely related in size to individual segment size. Though it is possible that neuropodia did exist in *D. costata*, it is clear that no relative size increase accompanied the great increase in width of the segments as the worms diverged from a normal polychaete shape. Rather than that, neuropodia probably decreased in size and may have been totally lacking.

Direct evidence of internal structures is rare. Two partial composite moulds indicate parts of paired gastric caeca. One indicates dichotomous branching of the caeca around the pharynx in the anteriorly-curved segments (Glaessner and Wade, 1966, pl. 101, fig. 4). The other has unbranched ridges (on the latex cast) in the mid-body region at right angles to the axis. Judging from the size of faint, segmental ridges in the anterior portion of the body, these caeca would have been spaced one pair per segment, and reached about 4/5 of the distance to the margins of the animal. In this specimen the major structures have less to little more relief than the sandgrains of the rock surface, and it has not been photographed successfully.

Less direct evidence of internal structures is provided by a number of specimens in which an axial ridge is present in the position of the intestine itself. In five specimens (Plate 5, figs. 1–4, Plate 6, figs. 1, 3, 4) the ridge is delimited by sharp furrows on either side. Two of these are relatively well-expanded specimens on which the notopodial-elytral ridges do not reach the axial ridge and one (Plate 5, figs. 3, 4) is intensely contracted. Perhaps these furrows result partly from the action of the most axial dorsoventral septal muscles (p. 176), for Plate 6, fig. 4 shows small pits along the furrow at the sides of the ridge where suture and furrow intersect, and where these muscles could be expected to exert most pull. These furrows are most pronounced on the least and most contracted specimens; on moderately contracted specimens the axial ends of the notopodial-elytral ridges are juxtaposed over the axial ridges (when these are present) and the axial ridges are less clearly delimited, though often quite prominent. As an axial ridge maintains an approximate width related to segment number (i.e. general size) regardless of the degree of expansion or contraction of the bodies, it must be due to an internal structure, and to one that is not always present. It is here considered evidence of a filled intestine.

The musculature of *D. costata* can not be observed directly but some data can be

assembled from studying the effects of contraction seen in some of the fossils. In order of frequency these effects produced:

- (1) Worms which have contracted, where later buried, from their maximum expansion by shrinkage inward all around the periphery. Contraction is often greater towards the rear end.
- (2) Worms which show one or more strong annulations, the only or outer one of which is a short distance inside the periphery (Plate 5, fig. 3, Plate 6, fig. 3; Sprigg, 1947, fig. 7, pl. 7, fig. 2; 1949, fig. 10, pl. 18, fig. 2, pl. 19, fig. 2; Harrington and Moore, 1956, fig. 14 (1a, c)).
- (3) Worms which are transversely contracted, the surfaces of segments being thrown into small crenulations which may be aligned from segment to segment but are interrupted by smooth lines along the sutures (Plate 5, figs. 3, 4). This form of contraction is usually accompanied by (2) but either can occur alone.

It is legitimate to assume the presence of the basic polychaete musculature of circular, longitudinal and septal muscles, and to consider how they may have been adapted as the width of the worms increased. There are several examples of flattened polychaetes (Clark, 1962) in all of which the 4 longitudinal muscles are spread as flat sheets against dorsal and ventral surfaces, and these have strands of dorso-ventral musculature incorporated in the septum. *S. arcticus* (Manton, 1967, figs. 2, 3) carried these adaptations to extreme; the longitudinal muscles have become diffusely scattered strands spaced more or less equally across top and bottom of the coelome, and the septa are represented mainly by dorso-ventral muscles and form sheets only in the upper part of the body below the notopodial-elytral ridges. From its preservation as impressions, *D. costata* was a rather tough worm, and the musculature necessary to move the larger specimens in particular can scarcely have been weak. It seems likely that the reduction of the longitudinal musculature had not proceeded as far in *D. costata* as in *S. arcticus*, but even parallel strips of muscle functionally roof and floor the coelome. Any acceptable model for longitudinal muscle distribution in the flattened, ovate bodies requires the muscles to curve in arcs which become progressively flatter from lateral to medial position. Contraction of these muscles alone would shrink the worm in area and increase its thickness. The two large specimens shown in Plate 5, fig. 1 are of almost the same segment number, the larger has 61 segments, the smaller probably 66. Both contracted *in situ* from their maximum size and were buried at the same time while still fresh. With no other pair of specimens is it possible to eliminate so many of the chance factors in preservation. While the larger specimen has contracted by nearly $\frac{2}{7}$ of its width the reduction of its length is only $\frac{1}{8}$, its individual segments are quite widely expanded and it has been compressed relatively flat; in comparison, the smaller specimen has more arched segment surfaces, its notopodial-elytral ridges are less regularly disposed, closely apposed in the centre, and the sutures are deeply depressed. In all, the differences between these 2 specimens are open to explanation as due to differing degrees of expansion of the individuals at the time of burial. Both specimens are normally preserved in comparison with other material. As their segment-number is close, the assumption that their fully expanded size would have been similar seems justifiable as a means of roughly estimating normal expansion and contraction. The maximum expansion of the larger specimen was not quite double the

present length and width of the smaller specimen; from this it would appear that a 2 : 1 ratio of expanded to contracted length and width was normally attainable. While strong contraction tended to produce an oval outline, Plate 5, fig. 1a indicates that contraction did not have to be uniform in early stages, at least when the animals were in contact with the ground.

The large-scale wrinkling (2, above) and minor crenations (3) cannot be explained by the action of longitudinal muscles. Circular muscles could be invoked to explain (3) if, as von Graff showed for *S. arcticus* (1888, pp. 31–2, fig. 6, pl. 1, fig. 11), they were not equally distributed. There seems no other likely explanation involving these muscles.

Of the large-scale wrinkles (2) the outer or only one occupies a relatively constant position a short distance inside the edge of the body. Plate 5, figs. 3, 4 show that in very contracted specimens the outer edges are not involved in the major wrinkles or minor crenations. Perhaps this area was formed by the notopodial fans, rather than the body edge, and the first large wrinkle marks the actual body edge (see also Plate 6, fig. 3). If this was so, the notopodial fans were fused together laterally. The muscles effecting this wrinkling are still unidentified but with the total or functional loss of neuropodia many muscles in these areas would have been reduced, lost or transformed in function and structure. Some transverse septal musculature could also have existed.

GROWTH

The smallest specimen is 3·8 mm long by 3·6 mm wide (Plate 1, fig. 8). It has 7 body segments, 2 angled forward, 1 transverse, 4 angled back toward a small, triangular pygidium. The next in size has 10 segments and is 4·8 mm long by approximately 5 mm wide; 3 of its segments curve anteriorly (Plate 5, fig. 7a, b). As more segments are added, more come to curve anteriorly (Plates 5, 6). Manton (1967) discussed a similar growth-series in *Spinther* in terms of increasing 'cephalization', for there the segment-number is relatively low and at least most of the forwardly curved segments have their central septal musculature involved in everting the pharynx. In *Dickinsonia* the increase in number of curved segments is not adequately described by this term, for the majority of the forwardly curved segments in larger specimens were too far from the pharynx to have been modified, though the more anterior gastric caeca do fuse together at either side of the pharynx, in the only specimen in which they are known. This suggests a comparable degree of 'cephalization' to that attained by *Spinther*. The forward curvature is better regarded as evidence of differential growth rates, the newer segments growing faster than the older ones and forcing them forward. If the newer segments had ceased to out-grow the older ones, forward curvature would have ceased, as happened in *D. elongata* where this change, plus continued growth, results in the immense number of transverse segments and huge size.

As the animals enlarged, the pygidium and pre-pygidial area where new segments were budded off must have increased in overall size also. The surface crinkling of a number of specimens is aligned in fine furrows the outer of which are intraperipheral, while progressively inner furrows arise from just posterior to the earliest segments (Plate 5, fig. 3), to about mid-body; they fade out on the small posterior segments. They are here considered evidence of the formation of increasing numbers of the muscles that contracted to cause the crinkling, as the pre-pygidial zone of segment generation gradually increased in size.

***Dickinsonia elongata* Glaessner and Wade, 1966**

The holotype of *D. elongata* was a juvenile specimen chosen because it was the only one which had both head and tail (Glaessner and Wade, 1966). Two almost complete adults and some more fragmentary specimens have now been discovered at Brachina Gorge and fragmentary specimens at Mt Scott Range and Mayo Gorge (Wade, 1970; this paper, Fig. 1). The smaller of the two is shown on Plate 7, fig. 2; the larger presents considerable difficulty in collecting. It is indistinct at the anterior and lacks the posterior few centimetres. A cast taken *in situ* is 45 cm in incomplete axial length and 17 cm in maximum width; about 280 segments are present. The specimen was first observed high in the cliff, with its complete posterior end exposed on the base of a thick yet badly fractured bed of sandstone and its mid-length to anterior end covered by a moderately thick bed. Since then, a private collector has cleared the lower bed, exposing the whole worm, and tried to chip the fossil from the bed on the base of which it occurs, destroying the posterior end. From memory, only 5–10 cm have been lost; the original worm probably had about 320 to 340 segments. Although fragmental worms which may have been larger than this are known, this is the largest nearly complete worm. The smaller nearly complete specimen was collected by R. J. F. Jenkins, University of Adelaide; its anterior end and most of the body are quite clear, though it is folded over at the posterior after 270 segments (Plate 7, fig. 2). Its probable length was 38–39 cm, maximum width is 13·8 cm. By analogy with *D. costata* this specimen is moderately contracted and in dorsal view. The ridge thought to be due to its intestine is 4 mm wide where its edges are most distinct, 6–8 cm from the anterior end of the worm. The anterior segments are short and narrow relative to *D. costata*, as was suspected from study of the slightly damaged holotype. From the proportions of the anterior segments of T54; 2050 it seems most likely that it is the anterior end of *D. elongata* and not *D. costata* (Sprigg, 1949, pl. 19, fig. 1; refigured (enlarged $\times 1\cdot45$) Harrington and Moore, 1956, fig. 14, 1b; Wade, 1968, fig. 28, illustrated a latex cast).

The holotype shows outer large ridges and folds toward the anterior, and minor crinkles some of which are aligned across the intervening sutures of several segments; these effects of muscular contraction are similar to *D. costata*. Additionally, the holotype and some other specimens show indications of notopodial-elytral ridges. *D. elongata* is thus closely similar to *D. costata* in all its known structures. It has not proved possible to distinguish the two species at small sizes. Presumably growth is prolonged in *D. elongata* which has 3 times as many segments as *D. costata*. The enormous width of some specimens similarly indicates prolonged growth of the whole body but the fact that the segments cease turning forward indicates that, except near the tail, they are all growing at the same rate. There is very little differential growth in length across the width of any one segment, except at the anterior of the animal.

There is no known indication of neuropodia in any specimen. On segment-length alone, it seems improbable that traces would be preserved if they were no more prominent than the possible traces rarely seen in *D. costata*. The retention of a structure already rudimentary at most in the more generalized form, is intrinsically unlikely. The locomotory adaptation seems more likely to be toward swimming than to benthonic movement (pp. 185–6).

II. *DICKINSONIA* WITH VERY SHORT SEGMENTS

In 1966, 16 specimens with very short segments were known, most of them fragmentary. Glaessner and Wade grouped all of them in one species centred on a rather broad form with segments finer than some specimens and coarser than others. Material now available shows that the forms with coarser and finer segments are both consistently elongate in shape, with many segments nearly parallel-sided, while the holotype of *D. tenuis* is almost as broad as long, and has centrally-tapering segments. *D. tenuis* is here restricted to the broad, short-segmented forms resembling the holotype, P13792 (Glaessner and Wade, 1966, pl. 103, fig. 1).

BROAD FORM

Dickinsonia tenuis Glaessner and Wade, 1966

EMENDED DIAGNOSIS: Oval outline; numerous, very short, wide segments taper inwardly so that most slope either anteriorly or posteriorly and few are transverse; dorsal axial line a sharp furrow which may, in composite moulds, traverse a narrow axial ridge (?indicating a filled intestine) that underlies the inner ends of segmental ridges and furrows.

Four specimens are known, all from Ediacara; the holotype, one contorted specimen (Plate 7, fig. 3) decidedly smaller than the holotype, an anterior end of a specimen slightly broader than the holotype, and a posterior end slightly smaller than the holotype. The holotype is a fairly contracted specimen with segments of average length 0.34 mm adjacent to the axis and just posterior to the forward-curved, anterior segments. The anterior fragmental specimen is well expanded and its segments average 0.59 mm in this region. The contorted specimen, P13768, resembles the holotype but it is not possible to be certain which end is anterior and which posterior, as it is folded along the axis at the end which appears to have had the larger segments. This obscures both their actual dimensions and their shape near the axis. The exposed end has rather small segments which are nevertheless U-shaped like an anterior end. Segments average 0.42 mm long adjacent to the axis. The average segment-size for fairly large specimens is thus in the vicinity of 20–30 segments per centimetre in the axial anterior region. At their longest (near the tips) the variable angles of the segment crests provide evidence of notopodial-elytral ridges like those of *D. costata*, although they are too small to be clearly seen. The axis on all specimens is a narrow furrow such as typifies dorsal sides, but on the contorted specimen (Plate 7, fig. 3) this furrow traverses a narrow axial ridge, in proportion as narrow as in *D. costata*.

NARROW FORMS

These *Dickinsonia* are narrower in proportion to length than *D. tenuis* and their segments do not taper toward their centres in a comparable fashion. They vary from a rather rare, evenly segmented form with a relatively narrow axial ridge and relative freedom from local distortions to a form which is generally smaller and generally has shorter segments, a relatively wide axial ridge, and rather variable outlines. The larger individuals of this kind have the same range of lengths and segments/cm as the evenly segmented form.

The question of whether all these short-segmented, elongate forms are one or two species is not easily settled. It is difficult to find comparable measurable characters because of the variability and incompleteness of specimens. Overall length is seldom measurable but relative size can be estimated fairly reliably. The 16 measurable specimens have therefore been lettered in alphabetic order from apparent largest to smallest in Fig. 2 where three characters that can be measured in most specimens are plotted.

- (1) the number of segments/cm, measured close to the axis at the first segments not effected by anterior curvature; if it was necessary to take this measurement more to the posterior, where segments may have been slightly smaller, it is marked '?'.
(2) $\frac{1}{2}W$, the maximum width from axis to edge, measured perpendicular to both.
(3) WA, the maximum width of the axial ridge which is attributed to the filling of the intestine.

D has a very narrow axial ridge, which is partly closed to a thin peak by an inward push of the right side (Plate 6, fig. 5). The narrow ridge was a characteristic probably originally shared by A in which its sides are not abrupt but sloping like the compressed part of D, its estimated size is plotted in inverted commas in Fig. 2b. Besides the measurable characteristics, the 3 broadest specimens, A, D and F, have very even, clearly marked segmental grooves. The very flattened F has a broad axial ridge which is probably not wholly explained by spreading due to flattening (Fig. 2b). The remainder of the specimens have furrowing which is regular and appears segmental in some, or is characteristically irregular in others; where regular, it has the same frequency as the average for comparable less regular areas of one specimen, or comparable less regular specimens. Specimen F is to some extent transitional between specimens D and A on the one hand and the remainder of the specimens on the other. On account of its broad axial ridge it is perhaps best to regard it as the member of the main group which most clearly displays its segmentation, partly due to having been well expanded and still quite well preserved at burial. Thus viewed, the elongate, short-segmented *Dickinsonia* with large numbers of transverse segments fall into 2 disparate groups of 14 specimens and 2 specimens (A and D). An additional elongate but very fragmental specimen can also be assigned to the latter group but is too poorly preserved for description; these rare specimens are here described as *D. brachina* sp. nov. The 14 specimens are described as *D. lissa* sp. nov.

***Dickinsonia lissa* sp. nov.**

(Fig. 2; Plate 6, fig. 6; Plate 7, figs. 1, 4)

Dickinsonia tenuis Glaessner and Wade (part), 1966, p. 622.

Dickinsoniid worm. Glaessner and Wade, 1966, p. 628.

Unnamed Dickinsoniid worm. Wade, 1968, table 1.

MATERIAL AND PRESERVATION: 14 specimens from Ediacara Range. One very flattened positive composite mould, 4 partly negative and partly positive composite moulds, and 9 negative composite moulds (including the holotype). The grainsize of the sediment tends to blot out the finer surface features, particularly on small segments.

HOLOTYPE: F17466, from Ediacara Range (Fig. 2, P; Plate 6, fig. 6).

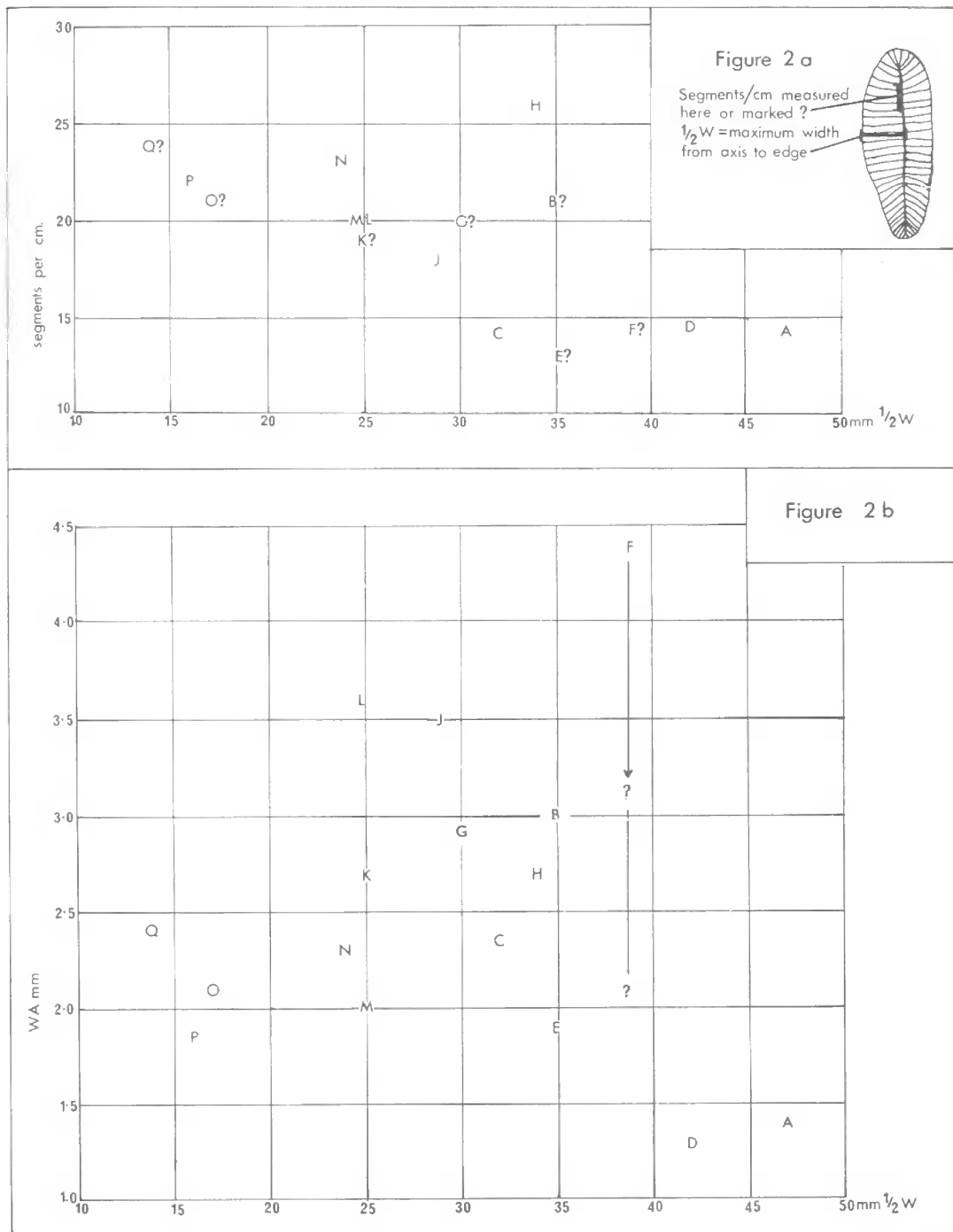


FIG. 2a, b: Dimensions of narrow *Dickinsonia* with short segments. Letters A-H, J-Q indicate specimens in estimated order of length. Whole specimens D, M, N, O, P. Maximum width from axis to edge, $\frac{1}{2}W$. Maximum width of axial ridge, WA. Specimen F is a totally flattened cast and the axial ridge appears to have spread in flattening. If a normal elevation is restored its plotted position on fig. 2b would move along the line indicated to a position between the question marks.

DIAGNOSIS: Elongate, rather narrow *Dickinsonia* with a relatively broad, prominent axial ridge (attributed to a filled intestine) underlying the inner ends of ridges and furrows which may be continuous from side to side or interrupted by a narrow, median depression as they cross the axial ridge (presumably a median depression indicates a dorsal side). Single lappets are sometimes visible at the outer ends of these segmental ridges. The lateral furrows may be irregular in shape, curving forward or back by up to one ridge-width particularly on sides with a median furrow. Where irregular, their average spacing agrees with their spacing in comparable, more regular, portions (most of the irregularity is thought to be due to the tilting of notopodial-elytral ridges).

DESCRIPTION: This species is the most variable in shape, its outlines in apparently undistorted specimens vary from elongate-ovate, widest near the anterior, to lenticular, widest at, or even behind, the centre of the body. Lateral furrows slope forward anteriorly and backward posteriorly, but in between almost half the segments lie nearly transverse in about half the specimens; the other specimens are either too fragmental to observe, or the majority of the segments slope either forward or back, and scarcely any are transverse. There is a prominent axial ridge on all specimens, broad enough to raise the inner ends of the lateral ridges and furrows in every example. On about half the specimens a median depression furrows the ridge and the segmental ridges are interrupted or offset across it (Plate 6, fig. 6; Plate 7, fig. 4). These specimens (Fig. 2, B, H, M, P, Q), are considered dorsal sides from comparison with *D. costata*. Three specimens are too poorly preserved to assess. The remainder of the specimens have intersegmental furrows which cross the axis without interruption and these are considered ventral sides (Fig. 2, C, F, J, L, N, O). On the few specimens which clearly show the edges of the body, the segments end in single lappets which appear to be a little longer than wide. The generally measurable characters have been plotted on Fig. 2 where specimens of *D. lissa* and *D. brachina* are ranked alphabetically in probable order of length. All the entire specimens of *D. lissa* (M, N, O, P on this figure) are in the size range 7.7–9.6 cm but there is an undistorted broken specimen (C) which is 16 cm in axial length and probably lacks 1–2 cm from the posterior end as well as most of one side. This specimen has 14 segments/cm close to the axis and just behind the anterior segments. The other large specimens, B, E, F, are measurable only further back; E and F also have 14 segments/cm but could be expected to have had only 13 segments/cm in a comparable, anterior position. B is very contorted and probably measured quite near the posterior end where it has 21 segments/cm (Plate 7, fig. 4). In general, the smaller specimens have the greater numbers of segments/cm, 26 being the largest number. This character must depend on the comparative size and on the state of expansion of the worms at burial, but the latter factor is self-cancelling as the more expanded worms are longer. A better measurement for size probably would be the total number of segments but there is no specimen in which the smaller segments can be counted, and many have large obscure areas. The number of segments lies between 200 and 300 in all specimens in which it can be estimated.

REMARKS: The very fine segmentation of *D. lissa* sp. nov. has lead to doubts as to whether its lateral furrows were truly segmental (Glaessner and Wade, 1966; Manton, 1967, p. 17). The presence of single lappets (presumably notopodial fans) at the outer ends of the lateral ridges is a strong argument in favour of segmentation. The lateral furrows

have restricted waviness and are noticeably less variable in shape on ventral sides than on dorsal sides. This gives an additional basis for inferring the presence of notopodial-elytral ridges in *D. lissa*.

The plasticity in general shape and in the angles segments make with the axis suggests a softer body texture than *D. costata*, *D. elongata* and *D. brachina*, and this is confirmed by the occasional presence of specimens preserved in positive relief on the bottoms of rock slabs, as in *D. tenuis* (Wade, 1968). The new species is distinguished from *D. tenuis* by its relatively narrower shape and the broad axial ridge attributed to the filling of its intestine. The fact that it is the only species to possess a constant axial ridge suggests it may have been a deposit feeder, while the others inclined more to grazing. It is usually smaller than *D. tenuis*.

The shape of the curved specimen of *D. lissa* (Plate 7, fig. 1) and the differing degree of expression of its anterior and mid-to-posterior segments, without a corresponding variation in the flattening of the edges and axis, suggest that the animal was overwhelmed by sediment while in differing states of contraction along its length, i.e. while still alive. It appears more laterally supple than the representatives of any other *Dickinsonia* species. This, taken in conjunction with the broad and constant axial ridge which suggests a sediment-filled intestine such as is known in many detritus-swallowing worms, makes a benthonic life for *D. lissa* seem very likely. There seems no theoretical limit on the minimum length of segments once there is no requirement for functional neuropodia. A major function of the septal musculature is holding dorsal and ventral sides together against the coelomic pressures engendered by the contraction of longitudinal muscles. The fact that *D. lissa* and *D. tenuis*, the two species whose preservation testifies to the least resistant body-tissues, are also those with the shortest segments suggests that it was profitable for the septa to be more closely spaced in the more delicate worms in particular.

***Dickinsonia brachina* sp. nov.**

(Fig. 2, A, D; Plate 6, fig. 5)

Dickinsonia tenuis Glaessner and Wade (part), 1966, p. 622.

MATERIAL AND PRESERVATION: One large partial specimen and possibly some small fragments from Ediacara Range. One whole and one fragmental specimen from Brachina Gorge. All are impressions on the bases of sandstone slabs.

HOLOTYPE: F17467 from Brachina Gorge (Fig. 2, D; Plate 6, fig. 5).

DIAGNOSIS: Elongate, narrow *Dickinsonia* with many transverse segments of similar width which do not taper toward their centres and which are less than half the length and width of comparable segments in *D. elongata*, so that the individuals are much smaller for a comparable segment-number. Axial ridge (?due to a filled intestine) relatively narrow.

DESCRIPTION: Only the holotype is complete, the partial specimen from Ediacara lacks most of its natural edges, part of its anterior end, and all the posterior end but its partial length is as long as the holotype. In both, the anterior segments are small and later segments increase in width for about one fifth of the body length, then reaching a near-constant width which is maintained until the segments commence to diminish in size (both length and width) toward the tail. As the length of all individual segments is practically constant

across their width, the segments are very slow to lose their forward curvature at the anterior and mid-body region, and slow to gain a posteriad slope at the tail. An axial ridge which uplifts the segmental ridges and furrows of the holotype is roughly constant in width at the anterior (1.3 mm) but pinched in the central part of the body where the right side is thrust slightly inward. The axial ridge is slightly wider (2 mm) in the tail region but as this would be the rectal part of the gut in *Spinther* there is considerable ground to suspect that this measurement would not be comparable with the others plotted as width of axis (WA) on Fig. 2, so the measurement taken at the anterior (1.3 mm) has been plotted for specimen D. The axis of the larger specimen (A in Fig. 2) is also elevated, its axial region in general is rather obscure but seems to have been only slightly broader than in the holotype. The holotype and probably the larger specimen are ventral sides. Only the holotype has its edges well enough preserved to show single lappets at the segment tips.

REMARKS: In its remarkably even length of individual segments this species resembles *D. elongata* although the fact that its early segments also scarcely taper toward their centres results in a relatively prolonged anterior curvature of the segments. Like *D. elongata* the body is of relatively constant width for half or more of its length. The resemblance between *D. brachina* (Plate 6, fig. 5, $\times 1$) and *D. elongata* (Plate 7, fig. 2, $\times \frac{1}{2}$) is exaggerated by the difference in magnification. The segments are vastly shorter than those of *D. elongata* and of comparable length to those of *D. tenuis* and *D. lissa*. They differ from those of *D. tenuis* by their constant individual length, as those of *D. tenuis* taper strongly toward their centres. The segments of large specimens of *D. lissa* have much more in common with *D. brachina* although they are not as regular and much more prone to local distortions, as if the bodies were softer. The principal measurable difference between *D. lissa* and *D. brachina* is that *D. brachina* has a much narrower axial ridge for its size than *D. lissa* (Fig. 2; contrast specimens A, from Ediacara, and D, the holotype, with the remainder of the specimens, all of which are attributed to *D. lissa*).

LOCOMOTION

Locomotion of errant polychaetes normally involves alternating waves of contraction of left and right longitudinal muscles (Chapman, 1958). This is aided by a 'power stroke' from the parapodia in at least several swimming forms (Clark and Clark, 1960); a similar movement is characteristic of walking forms. Sinuous lateral movement and parapodial locomotion are ruled out by the shape of *Dickinsonia* and the absence or reduction of its parapodia. Almost the only form of benthonic locomotory movement available to a worm of this shape appears to employ peristaltic waves of compression and extension. This requires functional septa, or a combination of septa and other structures which hinders the flow of coelomic fluid enough to allow temporary high pressure gradients to extend the animal. The usual posteriad slope on the notopodial-elytral ridges suggests that they were rigidly supported by spines and had 'roots' forming a septum in the upper part of the body like *Spinther* (Graff, 1888; Manton, 1967; the paper of Drasche, 1885, to which Manton referred is not available to me). The major part of any obstruction to coelomic flow would have been played by the septa. In *D. costata* the gastric caeca occupy perhaps half the length of the inner parts of segments in which they lie but much less toward the broad tips,

and they do not appear to reach to the edge of the body. There is no direct evidence of any other intra-coelomic structures but the worms were often surprisingly resistant to compression. They possibly contained a high proportion of 'glandular and other tissue and cells' as Manton (1967) and von Graff (1888), whose beautiful illustrations also show enormous masses of eggs or testes in the coelome, brought out in their descriptions of *Spinther*. In this event, the reduction in volume of the coelomic space in a contracted segment may have been enough to render the 'space' filled with cellular tissues, that is, a functional barrier to fluid movement, which did not require complete septa. The dorsal mesentery plus intestine would tend to provide a longitudinal barrier of more importance in worms with lateral movement like *D. lissa*.

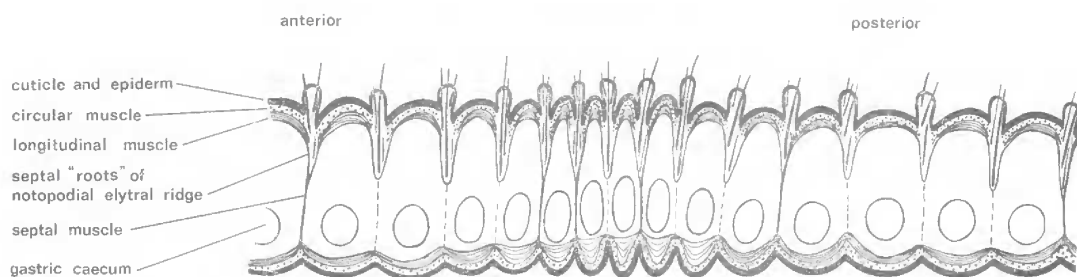


FIG. 3: *Dickinsonia costata* Sprigg, approximately $\times 5$. Hypothetical section to side of axis behind the anterior region, showing a wave of contraction passing from posterior to anterior. Based upon the 2 large specimens shown in Plate 5, fig. 1, the two composite moulds showing gastric caeca, and, for details of musculature, the modern polychaete *Spinther*. Simplified by omitting the gonads and other probable intracoelomic bodies which occur in *Spinther* and of which there is no evidence in the fossils.

Fig. 3 is a hypothetical longitudinal section of *D. costata* showing alteration in shape of segments during a wave of contraction. It is sited about mid-body and to one side of the intestine. The proportions of the notopodial-elytral ridges and the segments are restored from the larger specimens shown in Plate 5, fig. 1, and those of the gastric caeca from the specimen figured by Glaessner and Wade (1966, pl. 101, fig. 4) and the unfigured composite mould. The thickness of the body walls and depth of the septal roots of the notopodial-elytral ridges have been restored by comparison with *Spinther arcticus* (Graff, 1888; Manton, 1967); speculative intracoelomic structures have been omitted. It can be seen that, during contraction, several very incomplete septa plus intra-coelomic structures must have interposed a considerable baffle to the flow of coelomic fluids, and that if the contractions passed forward at a normal rate for polychaetes, 'leakage' through the incomplete septa could be needed to prevent overlarge pressure build-ups. In the diagram the lower surface has been shown as if flattened against the sea floor, because this must frequently have been the case. Although this may have been the main mode of locomotion of the early Dickinsoniids, and probably was the feeding locomotion of *D. costata* and more specialized forms, a rapid series of contractions would be quite likely to cause tapering segments to expand unequally and ripple the edges of the body so that the animals would tend to lift from the

sea floor. *D. costata* probably swam as Glaessner (1961) suggested. This is a possible type of swimming locomotion for *D. tenuis* which is the same general shape.

Increase in size frequently accompanies increased locomotory ability with its advantages for finding suitable feeding areas. It is hard to imagine a suitable food for *D. elongata* which was not obtained by grazing or detritus-swallowing, either of which would require benthonic movement of an errant polychaete, but the elongate, tough bodies seem particularly well adapted for swimming by waves of up and down contractions like a leech I have observed swimming with this motion, its body flattened dorsoventrally as described by Chapman (1958). If sinuous up and down movement also developed, some of the worms could have been quite rapid swimmers. This may be the reason why large numbers of equal, transverse segments arose, probably by convergence, in *D. elongata* and *D. brachina*. The ribbon-like and large *D. elongata* was morphologically so close to *D. costata* as to be indistinguishable from it unless 50 to 100 segments were present. *D. brachina*, like *D. elongata*, had a ribbon-like body with large numbers of near-equal segments between anteriorly curving head segments and posteriorly-curving tail segments; its extremely short segments suggest an affinity with *D. tenuis*. Small growth stages are not known from either species but extrapolation from the growth stages showing in the adults suggests even greater similarities between their young.

D. lissa, also possibly derived from the more generalized *D. tenuis*, may well have been benthonic (p. 183).

RELATIONSHIPS WITHIN *DICKINSONIA*

As in any group of five allied species from one short time-interval it is possible to argue about the similarity indicated by the distribution of characters. The systematic

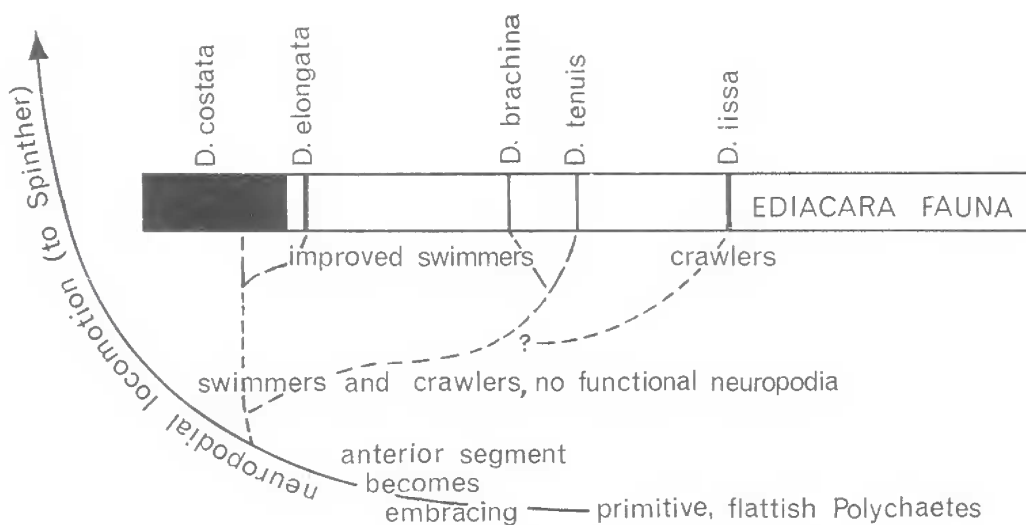


FIG. 4: Similarities and differences between the 5 known species of *Dickinsonia* expressed as a phylogenetic diagram. Relative frequency in the Ediacara fauna is represented by the width of the vertical black lines.

importance of the broad, consistently convex 'intestine' of *D. lissa* is endlessly debatable for the characteristic may not be very different from the relatively narrower and sometimes convex 'intestines' of the other species. Fig. 4 gives a preliminary assessment of the relationships. *D. costata* and *D. elongata* form one group on grounds of structure, segment-size and ontogeny. *D. brachina* and *D. tenuis* are almost equally close for comparable reasons if the segments are accepted as a record of ontogeny. *D. lissa* seems close to *D. tenuis* morphologically but the evidence of a broad, filled intestine and lateral suppleness suggests a more decided adaptation to benthonic life than any of the other species show. *D. lissa* has not sufficient preserved morphologic differences to be separated generically from the other species at this stage of our knowledge.

RELATIONSHIPS OF *DICKINSONIA*

Manton (1967) pointed out that 'The only mechanically convenient manner of obtaining great width to a flat segmented body is for the lateral parts of the anterior and posterior segments to fan forwards and backwards respectively. . . . By this expedient parapodia lie all around the margin of the animal and there is no extraordinary wide anterior face to the most anterior segment or posterior face to the most posterior segment.' This arrangement of parapodia has been achieved by ontogenetic increase in 'fanning forwards of the lateral parts' of the anterior segments in *Spinther*. As can be seen in many illustrations (e.g. in Day, 1967) this structure is incipient in the head region of many relatively broad worms, Palmyridae and Amphinomidae in particular. It has also been achieved (with loss of segmentation and concentration of musculature) by the Myzostomia. *Spinther* and *Dickinsonia* alone are known to have reached the limit possible to a segmented polychaete, complete fusion of the most anterior body segment along a line of contact anterior to the prostomium. This has allowed the anterior segments to achieve a relatively large size. For a mobile worm, there are advantages in not greatly diminishing (and weakening the musculature in) the anterior segments, advantages which would be greater the larger, and particularly the broader, the worm. The combination of selection for flatness and mobility seems enough to explain the encircling of the prostomium by the first body segment though size increase could also have played a part. Once the new adaptation was initiated, size increase in constant or broadening proportions would be sufficient to force the replacement of neuropodial locomotion. This order of events is suggested by the retention of neuropodial locomotion in *Spinther* and its loss in *Dickinsonia*.

The question of whether encirclement of the prostomium arose once or twice in the lines of *Spinther* and *Dickinsonia* could be debated on the ground that the detailed anatomy of *Dickinsonia* is poorly known, but the positive evidence is of relationship. The notopodial-elytral ridges are very similar and so are the gastric caeca, and the evidence for prostomia and mouths also points to a relationship. As *Spinther* is still specialized for neuropodial locomotion, though relatively inactive, and its 12-segment young stage described and figured by Manton (1967) is much less broadened than adult *Spinther* or the smallest known *Dickinsonia* (Plate 5, figs. 7, 8), the separation of these two stocks must have pre-dated the Ediacara fauna. Even at that date the habit of grazing on sedentary fauna was available to a rather small worm, though too restricted for a large and active form (Fig. 4). Its adoption

would almost guarantee the inhibition of locomotion in any group of worms taking it up. The differences between *Spinther* and *Dickinsonia* are thus most likely to have arisen by the ancestors of *Spinther* adopting an ectoparasitic life-habit which kept them small enough for neuropodia to function, and for which slow locomotion was adequate. This life habit has been available ever since. The particular niche favoured by the present species, which shelter and graze on sponges and within their larger cavities, has been available at least since Early Cambrian, and probably much longer. Other members of the ancestral group, probably spurred by size increase and certainly in an environment then free of predators on large, unarmed invertebrates, developed the new locomotion which characterized the Dickinsoniid line and permitted morphologic changes coupled with the diminution and loss of neuropodia. The temporary success of the innovation is indisputable but the niche for large, exposed and almost defenceless creatures was shortlived. The group does not appear to have been present at the time of formation of Early Cambrian sandstones lithologically similar to the Pound Quartzite.

As total morphologic obliteration of neuropodia is not certain in *D. costata* and is unlikely in its close ancestors, it is debatable whether *Dickinsonia* and *Spinther* are distinct at family level but the names Spintheridae Augener, 1913, and Dickinsoniidae Harrington and Moore, 1955, have already been coined and are useful for characterizing forms of such different life-habits that iterative evolution is extremely unlikely. The Amphinomidae, close to which *Spinther* is usually arraigned, include a large percentage of epifaunal browsers, but as Manton (1967) pointed out, the (basically relatively simple) proboscis of *Spinther* does not resemble any of the amphinomid or other polychaete stomodea illustrated and discussed by Dales (1962). Although it is less muscular and more voluminous, it is much closer to the *Myzostomum* stomodeum as figured by von Graff (1884, 1887; his monograph, 1877, is unavailable to me). This, of course, is even more dependant on protrusion by muscles than that of *Spinther*, as parenchyma replaces the (part-filled) coelome. The Myzostomia are much more specialized for parasitism than Spintheridae and their parapodia have evolved in a very different fashion; there is no suggestion of an ancestral relationship which merely pre-dated their loss of segmentation, rather, the similarity of the stomodea suggests a primitive stomodeal form which may have been quite wide-spread in the early Polychaeta. Myzostomid galls have been found in some quite early crinoids, so both these groups have respectably long time-ranges, the range of the Myzostomia being at least Ordovician–Recent. Manton considered *Spinther*'s stomodeum to be a specialized result of its ectoparasitic habit, so a careful comparison is required to evaluate the possibility of convergence in these two groups of ectoparasites.

If an ordinal subdivision of Polychaeta such as that recommended by Dales (1962) is used, Spintheridae and Dickinsoniidae presumably require their own order: Dickinsoniida Harrington and Moore, 1955, is available. Against this is the opinion of Day (1967) and others that no clear picture of major polychaete relationships has emerged. Evaluation of the taxonomic categories which portray the similarities and differences of *Spinther* and *Dickinsonia* can really be carried out only in the context of a thorough revision of 'Errantia' or Polychaeta in general, but their systematic position close to a root-stock which possibly included amphinomid and myzostome ancestors seems most probable.

Termier and Termier (1968, pp. 62, 150–1) proposed that *Dickinsonia* might represent an intermediate between the turbellarians and the molluscs, arthropods and (through *Tribrachidium* as a 'nymphoid') the echinoderms. *Dickinsonia* is quite unequivocally placed as a generally primitive polychaete, specialized in respect of its broad, flat shape, encircled prostomium, and its locomotion, but derived from ancestors with biramous parapodia and a more normal, narrow, elongate shape (characteristics of which *Spinther* provides living evidence). It cannot be regarded as a more likely candidate than any other polychaete for a 'missing link' which may unite all phyla with trochophore larvae (or derivatives) to a more primitive group. The Ediacara fauna in general appears too young to be the repository of links between many phyla. Coelenterates, annelids and arthropods were quite diversified by that time (Glaessner, 1971).

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